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Department of Biology, Liverpool Polytechnic, Liverpool, U.K.

The biology of mites from beech woodland soil[1])

MALCOLM LUXTON

With 4 figures

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1. Introduction

Hestehave beech wood near Ronde in East Jutland, was selected as the primary site for the Danish IBP investigations into the productivity of terrestrial ecosystems. Work began in earnest in 1968 and continued for three years until 1971, studies being made concurrently on the ecology of plant, animal and microbial populations. At the same time environmental variables such as temperature, rainfall and soil moisture were continuously monitored.

The mites or Acari formed a significant proportion of the soil biota in this beech wood, as they do in most soils. The Cryptostigmata were a particular focus of attention, but data were also gathered on the species populations of the other orders present for one year between March 1969 and March 1970. The detailed ecology is discussed elsewhere (LUXTON 1972, 1975, 1981 a—g; HERTZ 1971) and this paper seeks to summarise the information.

2. The site

The Hestehave Project was located within a 3 ha stand of 90 year old beech trees (*Fagus sylvatica* L.) situated near Rønde, about 30 km north of Aarhus, East Jutland, Denmark. The dominant species of the ground flora were *Anemone nemorosa* L., *Melica uniflora* RETZ., *Asperula odorata* L., *Hordeum europaeum* (L.) ALL., and *Carex sylvatica* HUDS. The humus fabric was a mull, with a friable sandy topsoil and a more clayey subsoil. The *p*H of the litter was 6.1—6.9 and of the mineral soil 4.2—7.6. Annual tree litter fall was between 435 and 535 g d wt m^{-2} (NIELSEN 1977) and organic matter input from the ground flora was 161.5 g d wt m^{-2} yr^{-1} (HUGHES 1975). Total precipitation for the mite sampling period was 472 mm, and mean annual temperature at the soil/litter interface was 6.8 °C.

A study area measuring 60 × 100 m was selected from the 3 ha site and 28 random plots measuring 10 × 10 m were marked out within it. Each month one subsample of 10 cm^{-2} was taken from each of these plots to a depth of 6 cm in the soil. The litter and the soil were extracted separately in a high gradient extractor of the Macfadyen type (PETERSEN 1978; LUXTON 1981 a). Soil temperature was continuously recorded at three points in the soil and litter horizons using thermistor sensors, and integrated to give monthly means. Monthly soil moisture measurements were made routinely and figures for monthly precipitation were obtained from a meteorological station situated 10 km from the site.

3. Dominance and frequency of the species populations

The soils of Hestehave beech wood contained 175 species of mites, 66 being Cryptostigmata, 66 Mesostigmata, 40 Prostigmata and 3 Astigmata (Table 2). Twenty-one species appeared to be of particular numerical importance (Table 1), appearing in more than 25 % of sample units and each constituting more than 5 % of all individuals in their order. Fewer than 10 % of species were energetically significant.

The Phthiracaridae may be considered as the most important family of mites in these beech wood soils. They accounted for almost 50 % of mite biomass, and *Steganacarus spinosus* (SELLN.) was the most significant phthiracarid species from the point of view of numbers, biomass, energy content and respiratory metabolism.

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1) Contribution from the Danish IBP, section PT.

Table 1. The most frequent and dominant species of each mite order

1. Cryptostigmata
Achipteria coleoptrata (L.)
Belba corynopus (HERM.)
Ceratozetes gracilis (MICH.)
Oppia subpectinata (OUDS.)
Oppiella nova (OUDS.)
Steganacarus magnus (NIC.)
Steganacarus spinosus (SELLN.)
Suctobelba spp.

2. Prostigmata
Eupodes sp. 1
Eupodes sp. 2
Microtydeus sp.
Nanorchestes arboriger (BERL.)
Tarsonemus sp. 1

3. Mesostigmata
Eviphis ostrinus KOCH
Holoparasitus stramenti KARG
Paragamasus lapponicus TRÄG.
Paragamasus truncus SCHWEIZ.
Uropoda (Cilliba) cassidea HERM.
Veigaia nemorensis KOCH
Veigaia pusilla BERL.

4. Astigmata
Rhizoglyphus echinopus FUM. et ROB.
(sensu HUGHES, 1961)

Note: More than 5 % of all individuals in that order: found in more than 25 % of all sample units.

Table 2. Data summary (m^{-2}) for the orders of Hestehave beech wood soil mites

	Cryptostig.	Prostig.	Mesostig.	Astig.	**Totals**
Density	34,512	20,480	10,151	2,253	**67,396**
Biomass mg d wt	253.3	3.7	139.6	4.8	**401.4**
Respiration KJ yr^{-1}	11.7	0.8	18.6	0.6	**31.7**
No. species	66	40	66	3	**175**

4. Density (Table 2)

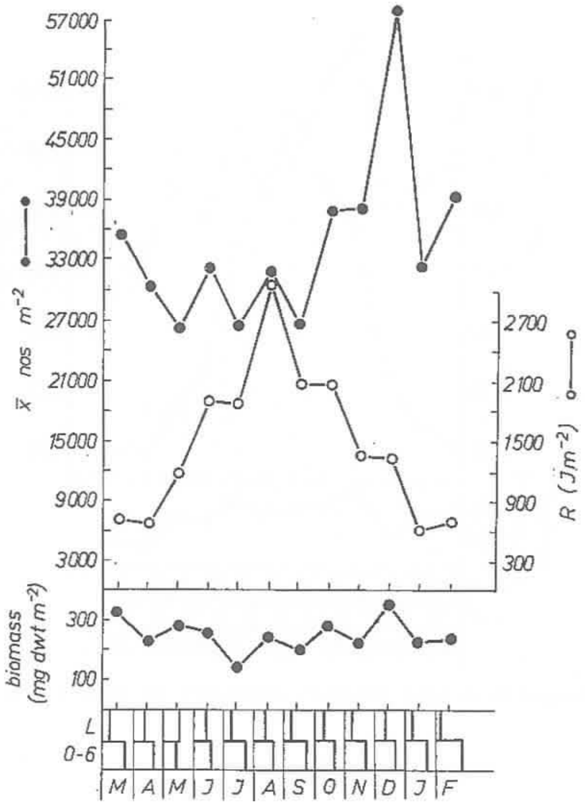
The annual monthly mean density of mites in Hestehave soils was 67,396 m^{-2}. The Cryptostigmata constituted the most abundant order with an annual monthly mean of 34,512 m^2 (range 26,107—58,071). The Prostigmata were the next most numerous with 20,480 m^{-2} (range 7,643—40,143) followed by the Mestostigmata (10,151 m^{-2}, range 6,234 to 14,842) and the Astigmata (2,253 m^{-2}, range 536—5,643). The relative density of Cryptostigmata : Prostigmata : Mesostigmata : Astigmata was therefore approximately 15 : 9 : 5 : 1.

Seasonally the Cryptostigmata were most numerous in winter and least in summer (Fig. 1). Prostigmata density fluctuated the most of any order (Fig. 2) but generally community numbers were greatest in winter and least in spring. Mesostigmata numbers were highest in early summer and lowest in the winter (Fig. 3) whereas the Astigmata density peaked in winter/spring and was lowest in summer/autumn (Fig. 4). In general the numbers of Mesostigmata were high when the Cryptostigmata and Astigmata numbers were low and vice versa. On the other hand, the Prostigmata and Cryptostigmata fluctuated together except for a Prostigmata density surge in summer which was not matched by the Cryptostigmata.

The dynamics of the Cryptostigmata community may be associated with both precipitation and litter fall. The main density peak in December coincided with the peak of litter input and followed the peak period of annual rainfall. In general it seems that rainfall may stimulate the progression of development so that the new stages may exploit the renewed resources represented by litter input. Members of the astigmatic community may also respond with an increase in numbers following rainfall peaks but the total mesostigmatic community showed no straightforward relationship with any measured environmental variable. The associations between these variables and density was not simple for the Prostigmata either, with some peaks following rainfall or litter input but with others seemingly unassociated.

Fig. 1. Seasonal changes in density, biomass, respiratory metabolism and depth distribution for the Cryptostigmata.

Fig. 2. Seasonal changes in density, biomass, respiratory metabolism and depth distribution for the Prostigmata.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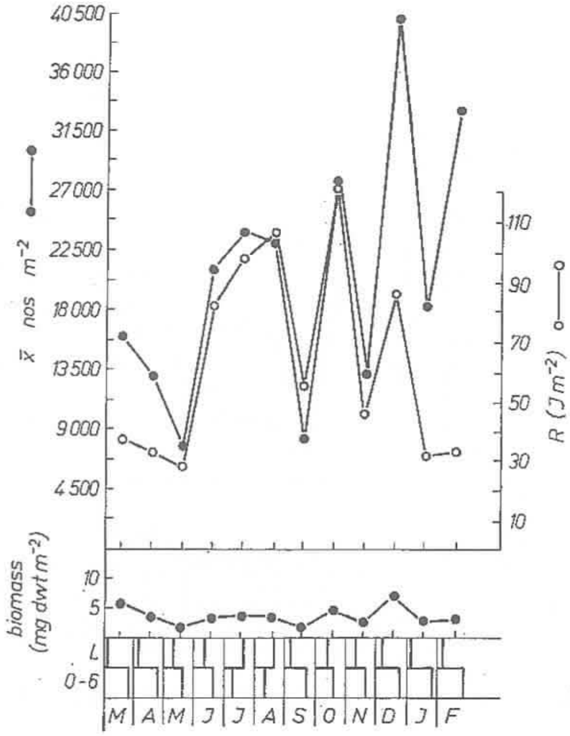
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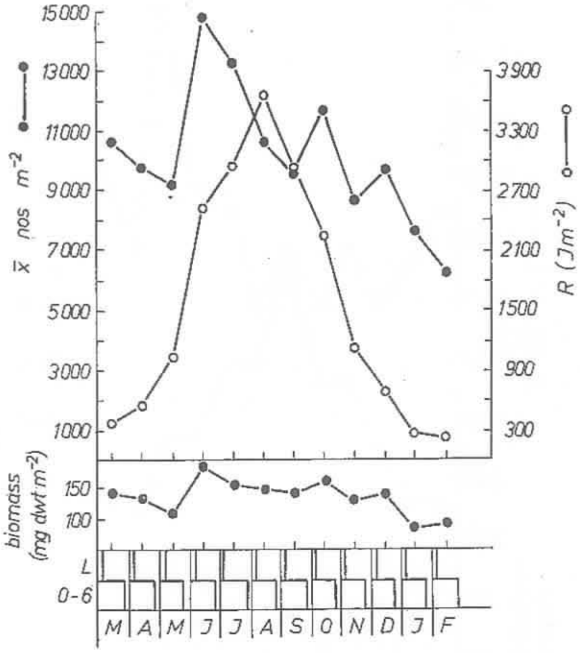

Fig. 3. Seasonal changes in density, biomass, respiratory metabolism and depth distribution for the Mesostigmata.

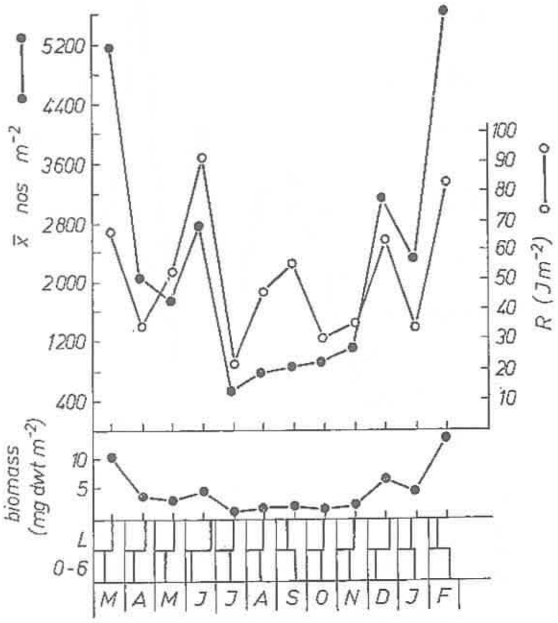

Fig. 4. Seasonal changes in density, biomass, respiratory metabolism and depth distribution for the Astigmata.

5. Biomass (Table 2)

The mean monthly biomass of mites in Hestehave soils was 401.4 mg d wt m^{-2}. Of this total the Cryptostigmata represented the most significant proportion with 253.3 mg d wt m^{-2} (range 149—358). The Mesostigmata contributed 139.6 mg d wt (range 86.5—194.9), the Astigmata 4.8 (range 0.9—13.6), and the Prostigmata 3.7 (range 1.6—7.3). Thus the biomass of Astigmata was greater than that of Prostigmata despite the fact that numbers of the latter were nine times greater than the former. Furthermore, the Mesostigmata, with half the numbers of Prostigmata, represented thirty-eight times their biomass. The average dry weight of a mesostigmatic mite (all stages) was 14 μg, of a cryptostigmatic mite 7 μg, of an astigmatic mite 2 μg, and of a prostigmatic mite 0.2 μg. Seasonal variation in community biomass did not always perfectly correspond with fluctuations in community numbers.

6. Respiratory metabolism (Table 2)

The annual total of energy dissipated in respiratory metabolism by the mites was 31.7 KJ m^{-2}, which represents only 0.34% of the tree litter input. The mesostigmatic mites were responsible for the greatest share at an estimated 18.6 KJ, which probably results from their behaviour as active carnivores. The Cryptostigmata also contributed a high proportion of the total at 11.7 KJ (in this case a consequence of their dominant numbers and biomass), with the Prostigmata at 0.8 and the Astigmata at 0.6. This time, the Prostigmata, with a lower biomass than the Astigmata, contributed rather more to the total community metabolism, possibly the results of their greater activity.

On the whole, the seasonal respiratory metabolism of the Prostigmata reflected community density changes rather than temperature. The Cryptostigmata and Mesostigmata, however, with a less erratic seasonal pattern of community density change, showed a peak metabolism out of phase with peak density. In both orders this occurred in the warmest month of August. The peak community density of Mesostigmata occurred before this event (in June) and the peak density of Cryptostigmata occurred subsequent to it (in December). The Astigmata showed an intermediate pattern, community density on the whole parallelling the community metabolism, except in the summer when numbers were low and respiratory metabolism showed a rise.

7. Depth distribution (Table 3)

The Astigmata were more abundant in the litter but the Cryptostigmata, Prostigmata and Mesostigmata were all more abundant in the soil. The astigmatic community became more abundant in the soil during the summer and the winter (Fig. 4) which was probably a reflection of a redistribution of one population, namely that of *Rhizoglyphus echinopus* Fum. et Rob. (sensu Hughes, 1961). The prostigmatic community became relatively most abundant in the litter layer during the summer months (Fig. 2), and the cryptostigmatic community in the spring, but there was little evidence of such redistribution among the Mesostigmata. More precise analyses of species populations reveal the likelihood of seasonal vertical migrations among certain species of every order.

Some mite species were almost totally confined to a narrow soil horizon for their entire life-cycle and rarely migrated vertically. Other species may be considered characteristic of

Table 3. Percentage depth distribution of the annual monthly means of mite orders in Hestehave soils

Order	Litter	0—6 cm soil
Cryptostigmata	26.5	73.5
Prostigmata	32.5	67.5
Mesostigmata	15.7	84.3
Astigmata	56.3	43.7

a particular horizon, but nevertheless migrate seasonally, and a very few ranged throughout the upper soil layers at will. At Hestehave most individuals were to be found in the litter and the top 6 cm of mineral soil, but the community was most numerous in that zone where organic matter is being incorporated into the mineral soil.

Seasonal vertical migration definitely occurred in some species and may have represented a flight from unfavourable conditions (especially unfavourable temperature) and/or a strategy for resource exploitation. Frequently the relative depth distribution patterns of some oribatid juveniles and their adults may be ascribed to different food preferences, but gravid females of several species of both Cryptostigmata and Prostigmata may migrate to a different part of the soil profile in order to deposit eggs. Deeper living Prostigmata appeared to initiate fewest generations in the year whereas it was the litter-dwelling Cryptostigmata which had fewest generations.

8. Breeding biology

Among the Cryptostigmata the greatest numbers of eggs were carried by litter dwellers, the females of which bore eggs at all times of the year or at least overwintered as gravid adults. Parthenogenetic oribatids lived mostly below the litter layer and developed eggs in the spring. Thus, the seasonality of egg maturation patterns may well be species specific, some populations having gravid females at all times of the year and others only for limited periods. In general eggs were deposited during summer and early autumn which hatched following the autumnal peak of precipitation. For many oribatids egg-laying may occur throughout the year during favourable periods, but most could be categorised according to definite oviposition pulses. Some synthesised and laid eggs over a very short period of time but this was not a common trait at Hestehave. Some species appeared to take advantage of litter energy input in autumn to synthesise eggs which then overwintered in the body of the female.

Egg bearing and deposition also seemed to be seasonal in the Gamasina, mostly occurring in spring and early summer, although some parasitid species also carried eggs during autumn and winter. The *Cilliba cassidea* (HERM.) population (Uropodina), on the other hand, carried eggs in all months except September with a minimum in summer.

The females of the principal astigmatic species *(Rhizoglyphus echinopus)* bore eggs throughout the year except during the summer months. The two other species, however, bore eggs only briefly and during early and late summer respectively.

Many Prostigmata species initiated their main annual generation in the winter or autumn months and very few did so in the spring. Those Prostigmata initiating their main generation in the summer were characteristically located in the litter.

Development time for most prostigmatic mites may be considerably shorter than for species of the other orders and they had more generations per year. The Astigmata had 1 or 2 generations a year, the Mesostigmata generally 1, the Cryptostigmata 1 to 3 (single generations being the most common), and the Prostigmata 1 to 4 (with multiple generations being common). In the Cryptostigmata subsidiary cohorts may be established out of main phase by some species which can rapidly react to environmental changes favourable to them.

Cryptostigmata species may take a year or more to complete development from egg to sexually mature adult. The rate of population development may be dictated or modified by prevailing environmental conditions, and oribatids have developmental Q_{10} s between 1.5 and 4. Some appeared to regulate their production rate in order to amass energy reserves in their tissues to overcome periods of low food intake or to enable them to overwinter as gravid females in order that the new generation may take full advantage of the improving resources of spring. Some species may co-ordinate their life-cycles with seasonal food availability. Cryptostigmata spend about one-third of their development time in the pre-ecdysial resting stage, and the length of life-cycle can very considerably between species. The females of some species became gravid soon after attaining the adult stage, whilst others became adult in autumn and overwintered before lying eggs the following season.

In the Cryptostigmata, the Prostigmata, and the Mesostigmata the principal overwintering stage may be characteristic of species. Where it is present in ontogeny, the tritonymph rarely overwinters.

Phenological patterns may be controlled by seasonal changes in the environment rather than typical of mite species. Precipitation and litter input may be of particular importance in triggering gross population changes, whereas temperature and soil moisture may dictate population activity patterns. Thus, although mites have seasonal reproductive rhythms, these are modified by climatic variables which may not be predictable year from year. Therefore the most helpful ecological comparisons may be those associated with season of the year in general or, in particular, with climate or other environmental variables monitored in parallel with the populations. The least helpful are those made from extrapolations of laboratory data which are frequently unrealistic since laboratory studies are mostly made at elevated and constant temperatures with an excess of food and space and an absence of environmental interaction.

9. Nutritional biology

The soil mite community displayed a wide spectrum of feeding behaviour. The Cryptostigmata were either macrophytophagous, microphytophagous or panphytophagous, with zoophagy being comparatively rare. Cryptostigmatic mites have distinct feeding preferences which may be important from the point of view of their distribution in the soil profile. At Hestehave the juveniles frequently had different preferences from their adults, and several species were capable of digesting plant structural polysaccharides.

The Prostigmata contained species which were clearly carnivorous but others were probably mycophagous, phycophagous, or feeders on roots.

Some of the Astigmata also probably fed on subterranean higher plant tissue, although most were apparently mycophagous.

The Mesostigmata were nearly all zoophagous, capturing and consuming what they could. However some were more selective, and the Macrochelidae appeared to prefer carrion in laboratory feeding experiments.

Competition for energy resources amongs mite species populations appears to be avoided in a number of ways. Thus, mites may partition space and food, or exploit both resources to different extents at different times. Adults and juveniles of the same species may exist in different soil horizons, feeding on different food materials. Macrophytophagous oribatids share the year in regard to energy exploitation, certain species being more active at certain times than at others. Astigmatic mites may also adopt the same strategy. Panphytophagous oribatids seem not to compete to the same extent for food, presumably because they are more flexible in their nutritional response.

10. Conclusion

The mite community at Hestehave comprises some 175 species populations representing an extremely varied feeding behaviour. Nevertheless, the Acari must be considered as only a part of a complex food web, situated in the soil and frequently referred to as a decomposer industry, which effects dead organic matter reduction through trophic interplay, releasing energy in metabolism and maintaining a balance in the nutrient fluxes of terrestrial ecosystems. From the standpoint of direct energy mobilisation, mites assume little importance in these soils. However, for relatively little energy expenditure mites may efficiently synergise the activities of the decomposer microflora, and may be particularly significant for the breakdown of more recalcitrant substances and for the relocation of nutrients and microbes within the profile.

11. Acknowledgements

I am particularly indebted to Annette Hertz and Henning Petersen for allowing me to quote their unpublished data on Mesostigmata. I am also grateful to Henning Petersen and Mike Thomas for criticising the manuscript.

12. Summary

This paper reviews the main results of an ecological study on the mites of a beech wood soil made under the auspices of the Danish IBP.

The soils of Hestehave contained 175 species of mites: 66 Cryptostigmata, 66 Mesostigmata, 40 Prostigmata, and 3 Astigmata. 21 species appear to be of particular numerical importance, but fewer are of energetic significance. The Phthiracaridae (Cryptostigmata) is considered to be the most important family, with *Steganacarus spinosus* the most significant species from the point of view of numbers, biomass, energy content, and respiratory metabolism. Annual mean monthly density of mites was 67,396 m^{-2}, with the relative proportions of Cryptostigmata: Prostigmata: Mesostigmata: Astigmata at 15: 9: 5: 1, and annual mean monthly biomass was 401.4 mg d wt m^{-2}. Total respiratory metabolism was 31.7 KJ m^{-2}, which represents only 0.34% of the tree litter input.

The Astigmata were more abundant in the litter but the other orders were more abundant in the mineral soil. Some vertical redistribution of numbers seasonally was evident for some species of all orders. This appeared to represent a flight from unfavourable conditions and/or a strategy for resource exploitation. Some species moved elsewhere in the soil profile for oviposition.

A summary is provided of the more important elements of mite breeding biology and it is concluded that seasonal reproductive rhythms are modified by climatic variables, the timing of which may not be predictable from year to year. Precipitation and litter input may be of particular importance in triggering gross population changes.

Feeding behaviour is discussed, together with the ways in which mite populations appear to avoid competition for energy resources.

It is concluded that mites assume little importance in these soils from the standpoint of direct energy mobilisation but that for relatively little energy expenditure they efficiently assist in synergising the activities of the microflora, and may be particularly significant for the breakdown of more recalcitrant substances and for relocation of nutrients and microbes within the soil profile.

13. Literature

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Address of the author: Dr. MALCOLM LUXTON, Department of Biology, Liverpool Polytechnic, Byrom Street, Liverpool L3 3AF, U.K.